USE OF BURROW ENTRANCES TO INDICATE DENSITIES OF TOWNSEND'S GROUND SQUIRRELS

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Abstract: Counts of burrow entrances have been positively correlated with densities of semi-fossorial rodents and used as an index of densities. We evaluated their effectiveness in indexing densities of Townsend's ground squirrels (*Spermophilus townsendii*) in the Snake River Birds of Prey National Conservation Area (SRBOPNCA), Idaho, by comparing burrow entrance densities to densities of ground squirrels estimated from livetrapping in 2 consecutive years over which squirrel populations declined by >75%. We did not detect a consistent relation between burrow entrance counts and ground squirrel density estimates within or among habitat types. Scatter plots indicated that burrow entrances had little predictive power at intermediate densities. Burrow entrance counts did not reflect the magnitude of a between-year density decline. Repeated counts of entrances late in the squirrels' active season varied in a manner that would be difficult to use for calibration of transects sampled only once during this period. Annual persistence of burrow entrances varied between habitats. Trained observers were inconsistent in assigning active-inactive status to entrances. We recommend that burrow entrance counts not be used as measures or indices of ground squirrel densities in shrubsteppe habitats, and that the method be verified thoroughly before being used in other habitats.

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Assessment of evidence of animal activity may provide a cost-efficient means of indexing densities where mark and recapture techniques would otherwise be required. Ground squirrels are an important food resource for many predators. Thus, a technique for censusing ground squirrels that indexes spatial variation in population density and also indicates the magnitude of major population fluctuations would be useful in managing ecosystems for habitats, prey, and predators.

Several studies have correlated counts of burrow entrances with estimates of ground squirrel densities (*Spermophilus beecheyi*, Owings and

Borchert 1975; *S. columbianus,* Weddell 1989; Townsend's ground squirrels, Nydegger and Smith 1986). Nydegger and Smith (1986) reported a tight relation (simple linear regression, $r^2 = 0.89$) between numbers of burrow entrances and 5-year average population densities on the same 5 sites. In contrast, Powell et al. (1994) did not detect a consistent positive relation between aboveground counts of black-tailed prairie dogs (*Cynomys ludovicianus*) and high, medium, and low burrow entrance densities.

Our objective was to evaluate burrow entrance counts as an index of Townsend's ground squirrel densities in the SRBOPNCA in southwestern Idaho. This area contains one of the highest densities of nesting raptors in the world (U.S. Dep. Inter. 1979), and the primary purpose of the conservation area is "the conservation, protection, and enhancement of raptor populations and habitats . . ." (U.S. Public Law 103-64, 4 Aug 1994). Because Townsend's ground squirrels are important prey for many raptors in this area (Steenhof and Kochert 1985, 1988; Marti et al. 1993), management for raptors requires an ability to determine spatial and temporal population trends of the ground squirrels. Extensive wildfires have recently changed shrubland to exotic annual grasslands (Kochert and Pellant 1986) and have the potential to disrupt historical population norms of squirrels (Yensen et al. 1992).

Counts of burrow entrances along transects provide an efficient means of sampling over a wide area. Counts of burrow entrances on ≤300 transects each 5 × 400 m (60 ha total area) per annual season have been used as an index of ground squirrel density in the SRBOPNCA since 1977 (U.S. Dep. Inter. 1979, Nydegger and Smith 1986, Knick 1992, Yensen et al. 1992). These counts were conducted near the end of the active season for squirrels (mainly Jun and Jul) because the intent was to index the maximum densities of squirrels for the year. Maximum densities are greatly influenced by the densities of juvenile squirrels, and sampling earlier in the season would probably underestimate juvenile densities.

Burrow entrance counts would be useful if they varied consistently with differences in population density within and among habitats, and if they indicated the extent of a major population fluctuation. To evaluate the reliability of burrow entrance counts as an estimate of population density, we (1) compared area-wide counts of burrow entrances with estimates of Townsend's ground squirrel density on 20 sites for each of 2 years, (2) evaluated the repeatability of burrow entrance classifications among observers along transects and the stability of counts within the 10-week period required to conduct a useful burrow entrance census near the time of immergence, and (3) measured the persistence of individual entrances between years in different habitats, because differential persistence would lead to among-habitat bias in burrow entrance counts. In these analyses, we assumed that density estimates based on mark and recapture of actual animals were more accurate than more indirect estimates based on counts of burrow entrances.

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STUDY AREA

We conducted our study on the benchlands of the SRBOPNCA (43°N, 116°W), which is 900–950 m in altitude and 195,243 ha in extent. Topography was generally flat except for isolated buttes. Major native vegetative associations were characteristic of shrubsteppe communities: big sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*), and winterfat (*Krascheninnikovia lanata*). Precipitation on the benchlands was usually 20–30 cm/year. About 50% of the shrubland has burned since 1980 (Kochert and Pellant 1986). Burned areas were dominated by grasses and forbs rather than shrubs, including the native bunchgrass Sandberg's bluegrass (*Poa secunda*) and many exotic annuals.

METHODS

Densities of Ground Squirrels and Burrow Entrances

Ground Squirrel Abundances.—Livetrapping was conducted on 20 sites for 2 years (1992 and 1993) throughout the February-June active season of Townsend's ground squirrels. Most adult ground squirrels immerge into hibernation during late April and May, and juveniles immerge during June. Animals hibernate until emergence the following February. We selected site types to meet the broader objectives of our study of population dynamics and habitat-relations of squirrels. Ten sites were selected in areas that had been burned by wildfire within 7 years of the start of the study, and 10 sites were selected in unburned areas dominated by native shrubs. Of these shrub sites, 2 were dominated by winterfat, 2 by a winterfat-sagebrush mosaic, and 6 by big sagebrush. In 1993, supplemental food provided to ground squirrels on 2 burned sites was associated with relatively high densities of squirrels.

We placed Tomahawk wire-mesh livetraps in a grid arrangement, baited them with fresh apple $\leq$2 hours after sunrise, and checked them every 1–2 hours for 2–3 checks per day. Traps were closed during rain. Squirrels were marked with uniquely numbered passive integrated transponders (Schooley et al. 1993). In 1992, we varied the sizes of trapped areas among sites because squirrel densities differed substantially; our goal was to obtain an adequate number of captures on each site to estimate densities. We trapped 9-ha areas where ground squirrel densities had been low in 1991 (Van Horne et al. 1992, 8 sites), 4.5-ha areas where densities had been moderate in 1991(4 sites), and 2.25-ha areas where densities had been high in 1991(8 sites). One-day trapping sessions were conducted 6–8 days apart (except that trapping was suspended on sites with $\leq$2 adult females during the early phase of juvenile emergence) for a total of 11–20 trapping days on each site per active season. This protocol allowed for concurrent comparisons of densities and life-history information among the 20 sites. Where juvenile production was expected to be high, based on captures of reproductive females, we reduced the sizes of areas sampled (but not no. of traps) during and after juvenile emergence (late Mar–early Apr to Jun) so that we could continue to process trapped animals within 2 hours while minimizing trap saturation. Three 4.5-ha trapping areas were reduced to 2.25 ha, and 1 was reduced to 1 ha. All 2.25-ha trapping areas were reduced to 1 ha. In 1993, we expected moderate or low densities on all but the supplemental food sites because of a late-season drought in 1992, so we trapped 4.5-ha areas on all sites. Few juveniles emerged in 1993, so we did not reduce the sizes of trapped areas during the emergence period.

We estimated densities using methods for open populations based on the Jolly-Seber model (Seber 1982), which allowed for modeling of capture and survival parameters. We modified a PROC NLIN (SAS Inst. Inc. 1990) program (Burnham 1989) to allow such parameter modeling for the no recruitment case of the Jolly-Seber model. As advocated for survival rate analysis (Lebreton et al. 1992), several models were developed for each dataset, and estimates were obtained from the "best" model as determined by the criteria: (1) low (Akaike's Inf. Criterion [AIC], Akaike 1973; Anderson et al. 1994), (2) realistic model assumptions, and (3) realistic parameter values. We examined models for all combinations where both survival and capture rates were time-specific, were held constant, or were modeled as a linear or quadratic function of time. The model selected most often incorporated a constant survival rate and a linear function for capture rates.

In 1992, adult densities were based on data collected before juvenile emergence and grid shrinkage. In 1993, we used data for the entire season to estimate adult densities, because trapping data were sparse and grid sizes were not reduced at juvenile emergence. For both years, the model estimated adult abundances at the time of adult emergence (i.e., time 1), so estimates were comparable. Estimates of juvenile densities were the sum of juvenile densities estimated for the period of juvenile emergence, ending in early May, and a minimum number alive estimate of later juvenile immigrants (juv first captured after early May).

Area Estimation.—To obtain the effective area trapped for density estimates, we estimated a strip width (w) to be added to the naive trapping grid area using ½ the mean maximum distance moved (MMDM) for all animals captured $>$1 time in $>$1 trapping location. We used data on movements only from the grids that were $\geq$2.25 ha because measurements of maximum movements were biased on the reduced grids (1.0 ha). Our preliminary analysis indicated that movement distances did not differ between habitats ($P > 0.05$), so we combined data between habitats and tested for sex, year, and sex-year interaction effects with analysis of variance (ANOVA). We conducted separate ANOVAs for adult and juvenile squirrels.

Estimates of population density, by site, were obtained by dividing the age-specific population size estimates by the corresponding effective trapping area. Total densities used in comparisons were the sum of the age-specific estimates.

Burrow Entrance Densities.—We counted burrow entrances on the 20 sites during the first 2 weeks of June each year after most adult ground squirrels had recently immerged and most juveniles had not. We expected that this time period would include the maximum densities of entrances for the year and would provide the best index to overall squirrel densities (including juv). We counted entrances in adjacent belt transects that covered the entire trapped area. Criteria used to distinguish Townsend's ground squirrel burrows from those of kangaroo rats (*Dipodomys ordii* or *D. microps*) included a rounder and more vertical entrance, and, when it had not rained recently, the absence of tail drags characteristic of kangaroo rats. We enumerated both active and inactive entrances, as we thought that persistence of activity sign was probably weather-dependent, making counts of active entrances potentially inconsistent. Also, other small mammals (primarily least chipmunks [*Tamias minimus*] and kangaroo rats) may use otherwise inactive ground squirrel burrows, making them falsely appear to be active.

We described the predictability of ground squirrel densities from active and from total (active + inactive) burrow entrance densities using separate simple linear regressions. We performed analyses for all sites combined and separately for burned sites ($n = 10$) and shrub sites ($n = 10$). Analysis of covariance was used to determine the stability of the relation between burrow entrance counts and ground squirrel densities between years for all 20 sites.

Observer Bias and Within-Year Stability of Burrow Entrance Counts

We assessed the precision of estimates of burrow entrance counts and the potential bias among observers in classifying activity of burrow entrances at 10 5- × 400-m transects. Entrances were independently counted along transects by 2 teams each with 2 experienced observers. Rotation of the starting team was randomly determined. The second team started the transect after the first team had finished. The center line was delineated by a tape with consecutive 5-m segments identified. Each observer group mapped the location of all entrances within each 5- × 5-m segment along the strip. Precision was measured as the variance of $\hat{N}$ determined from from the 2-sample capture-recapture (Petersen) estimator (Seber 1982). This method assumed that (1) the population of burrow entrances was constant in size, (2) sightings were independent between different burrow entrances and different teams, (3) the probability of sightings was the same for each team but could vary between teams, and (4) mapping was precise so that each sighting was attributed to each team.

We tested for seasonal changes in burrow entrance counts over a 10-week sampling season by repeated sampling of 5- × 400-m calibration transects. We expected that numbers of active, inactive, and total burrow entrances might change because the sampling interval previously used to count entrances (Knick 1992) included the period of squirrel immergence, when the number of active squirrels declines. We established 5 transects in each of 5 habitats: winterfat, sagebrush, sagebrush-winterfat mosaic, and 2 burned-sagebrush habitats including a native perennial grassland of Sandberg's bluegrass and bottlebrush squirreltail (*Sitanion hystrix*), and a grassland dominated by cheatgrass (*Bromus tectorum*) and Russian thistle (*Salsola iberica*). These transects were sampled biweekly from 18 May to 28 July 1992. This time period spanned the typical period of historical counts of burrow entrances, and it also included the period (early Jun) when total counts were conducted on our 20 trapping sites in 1992–93. We also examined the mean number of entrances counted in randomly located transects not used for repeated sampling to determine whether these had a similar pattern of variation during the same time period. Habitat types were sampled evenly through the sampling period on the randomly located transects.

Among-Year Persistence of Burrow Entrances

Two trapping sites from each of 3 vegetation associations (winterfat, sagebrush, and burned sagebrush-native perennial grassland) were used to investigate persistence of burrow entrances. We randomly selected 50 ground squirrel burrow entrances each on the 6 trapping sites between 11 and 17 June 1992. Only burrow entrances that were neither caved in nor filled with debris were sampled. We marked entrances with

Table 1. Slopes (b), intercepts (a), and summary statistics (r^2, P) of simple linear regressions of Townsend's ground squirrel densities (ad + juv; no./ha; $\hat{D} = \hat{N}/\hat{A}$) on total ($B$) and active ($B_A$) burrow entrance densities (no./ha) for squirrels in the Snake River Birds of Prey National Conservation Area, Idaho, 1992–93.

Independent variable	Habitat	1992				1993			
		b	a	r^2	P	b	a	r^2	P
B	Burned	0.00	53.0	0.02	0.6805	0.00	8.2	0.04	0.5685
	Shrub	0.07	4.0	0.11	0.3495	0.01	2.9	0.01	0.7466
	Combined[a]	0.20	−9.3	0.51	0.0004	0.03	2.4	0.16	0.0803
B_A	Burned	−0.12	92.3	0.08	0.4364	0.04	7.7	0.10	0.3786
	Shrub	0.20	2.2	0.25	0.1394	0.07	1.6	0.07	0.4726
	Combined[b]	0.22	19.9	0.18	0.0622	0.07	3.3	0.24	0.0282

[a] Slopes differ between years (ANCOVA) $F = 21.1$, 1,36 df, $P < 0.001$.
[b] Slopes differ between years (ANCOVA) $F = 9.8$, 1,36 df, $P < 0.005$.

numbered aluminum tags attached to metal rods and recorded their locations. A single observer (RLS) selected most burrow entrances (289 of 300) in 1992, and he re-surveyed all burrow entrances from 5–10 May in 1993 and again in 1994. He recorded whether each burrow entrance persisted and whether or not it was active.

Persistence of individual burrow entrances may not have been independent within sites, so we used sites as independent samples in statistical tests. Thus, the persistence of total entrances refers to the proportion of entrances on a site that survived from 1992 to a subsequent year (classified as active or inactive in that yr), and the persistence of active entrances refers to the proportion of entrances on a site that survived from 1992 to a subsequent year (active only). We tested for differences between shrub sites ($n = 4$) and burned sites ($n = 2$) in persistences of total entrances and active entrances from 1992 until 1994 with Kruskal-Wallis tests.

RESULTS

Densities of Ground Squirrels and Burrow Entrances

Area Estimation.—For adults, maximum movements differed between sexes ($F = 4.04$; 1, 397 df; $P = 0.0450$) and years ($F = 10.15$; 1, 397 df; $P = 0.0016$) but there was no sex-year interaction ($F = 1.24$; 1, 397 df; $P = 0.2658$). Thus, we computed sex-specific yearly mean (±SE) strip widths for adults (1992: 23.43 ± 2.06 m and 21.78 ± 1.77 m for males and females, respectively; 1993: 31.32 ± 1.68 m and 25.58 ± 1.71 m for males and females, respectively). For juveniles, maximum movements were not influenced by sex ($F = 0.35$; 1, 69 df; $P = 0.5553$), year ($F = 1.11$; 1, 69 df; $P = 0.2961$), or their interaction ($F = 0.05$; 1, 69 df; $P = 0.8244$). Thus, we computed an overall strip width for juveniles (30.58 ± 1.88 m). Our results were consistent with those of Johnson et al. (1987) who used the same method for calculating strip widths for Townsend's ground squirrel and reported strip widths for ages and sexes combined of 34.7 ± 4.1 m and 34.9 ± 4.1 m for 1982 and 1983, respectively.

Ground Squirrel and Burrow Entrance Densities.—Densities of ground squirrels across the 20 sites were positively associated with densities of total and active burrow entrances (Fig. 1), but the correlations were significant only for total entrances in 1992 and active entrances in

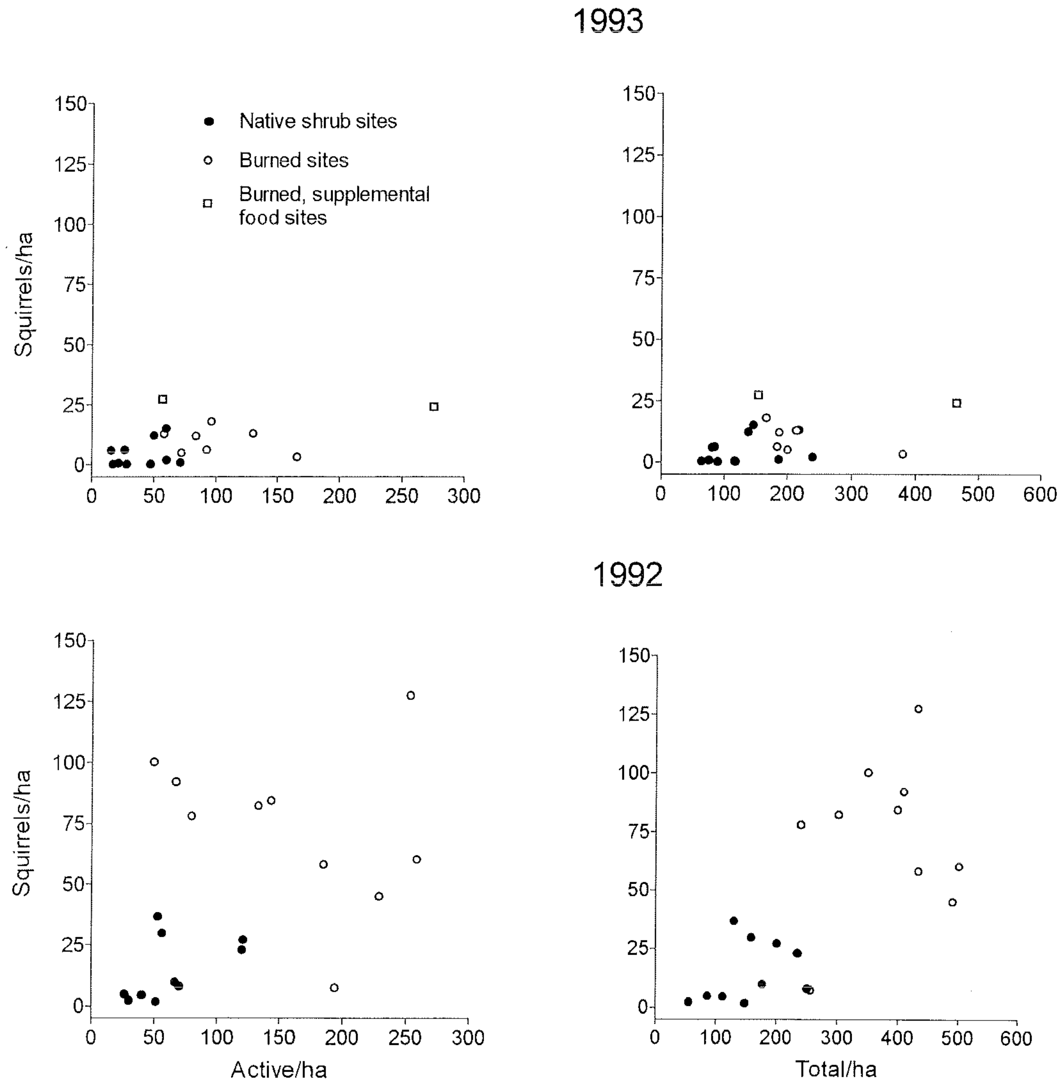

Fig. 1. Estimates of population densities for Townsend's ground squirrels as related to densities of active burrow entrances (Active) and total burrow entrances (Total) for 20 sites in the Snake River Birds of Prey National Conservation Area, Idaho, 1992–93. Note that X-axis is scaled differently for Active and Total burrow entrances. Regression coefficients and statistics are provided in Table 1.

1993. The slope of the relation was inconsistent among years (Table 1). Moreover, these significant correlations depended on pooling both shrub and burn sites in the analysis. Within habitat types, burrow entrance and ground squirrel densities were not significantly related (Table 1). Mean densities of squirrels and of burrow entrances were higher on burned than on shrub sites in both years (Table 2). Burrow entrance densities explained ≤25% of the variation in estimated ground squirrel densities within each habitat (Table 1).

Between 1992 and 1993, population densities declined 84% (SE = 4%) on burned sites and 79% (SE = 6%) on shrub sites (Table 2). Burrow entrance counts also declined between years, but not by the same magnitude. The decline in mean densities of total burrow entrances was only 42% (SE = 5%) on burned and 17% (SE = 8%) on shrub sites. Mean densities of active burrow entrances declined 21% (SE = 16%) and 28% (SE = 11%) on burned and shrub sites, respectively. Because of the unequal decline in ground squirrel and burrow entrance densities between 1992

Table 2. Densities ($\hat{D} = \hat{N}/\hat{A}$; no./ha) of Townsend's ground squirrels, total (B) and active (B_A) burrow entrances, and $B/\hat{D}$ in the Snake River Birds of Prey National Conservation Area, 1992–93. Each mean and standard error is for 10 study sites.

		1992		1993	
Variable	Habitat	$\bar{x}$	SE	$\bar{x}$	SE
$\hat{D}$	Burned	73	10.4	12	2.8
	Shrub	15	4.1	4	1.7
B	Burned	381	29.0	228	34.2
	Shrub	156	19.9	122	17.6
B_A	Burned	159	24.3	108	21.8
	Shrub	63	10.4	40	6.4
$B/\hat{D}$	Burned	8	3.1	73	43.3
	Shrub	23	7.6	234	99.4

and 1993, the ratio of total burrow entrances to densities of ground squirrel increased (Table 2).

Observer Bias and Within-Year Stability of Burrow Entrance Counts

The 2-person teams did not consistently detect the same number of burrow entrances within the 5- × 400-m strip transects. Total number of burrow entrances estimated per transect ($\hat{N}$ from the 2-sample estimator) averaged 42.7 and ranged from 14.0 to 100.4 for the 10 calibration transects. The variance of $\hat{N}$ ranged from 0 to 16.4 on 9 transects, and was 71.3 on 1 additional transect. Transects with the largest variance (and greatest difference in detection between the 2 teams) were located in big sagebrush habitats.

Teams differed in assigning activity status to 28% of 188 burrow entrances commonly mapped on all transects. Within each transect, the proportion of burrow entrances with different activity assignments ranged from 0 to 44%. Observers were consistent in classifying Townsend's ground squirrel and kangaroo rat burrows; only 3.5% of 195 burrow entrances commonly mapped received different species assignments (this was a test of consistency, not a test of correct classification).

Total entrances declined through the sampling period for each calibration site and for the mean number of burrow entrances counted on random sites (Fig. 2). Active entrances decreased and inactive entrances increased during the season. Total entrances declined sharply after mid-June, when nearly all ground squirrels had immerged.

Among-Year Persistence of Burrow Entrances

The persistence of burrow entrances from June 1992 to May 1994 was habitat-dependent (Table 3). The persistence of total entrances on the 4 shrub-dominated sites was greater than for the 2 burned sites ($\chi^2 = 3.429$, 1 df, $P = 0.0641$). The persistence of active entrances (Table 3) was also greater on the 4 shrub sites than on the 2 burned sites ($\chi^2 = 3.529$, 1 df, $P = 0.0603$). The lowest persistence of burrow entrances was on the only supplemental food site that we sampled (Burn 7a), where population density increased between 1992 and 1993, in contrast to the other sites where population density decreased over this period (Table 2). Densities of ground squirrels were higher on most burned sites than on shrub sites (Table 2), but there was no associated trend toward higher burrow entrance persistence on burned sites.

Table 3. Proportion of burrow entrances of Townsend's ground squirrels classified as active in mid-June, 1992 that were absent, inactive, or active on 5–10 May in 1993 and 1994.

				Entrance persisted	
Site	Year	n[a]	Entrance absent	Inactive	Active
Winterfat (1a)	1993	50	0.02	0.80	0.18
	1994	50	0.16	0.46	0.38
Winterfat (1b)	1993	50	0.10	0.66	0.24
	1994	50	0.20	0.58	0.22
Sagebrush (2a)	1993	50	0.04	0.38	0.58
	1994	48	0.19	0.44	0.38
Sagebrush (2b)	1993	50	0.02	0.38	0.60
	1994	49	0.10	0.59	0.31
Burned sagebrush (7a)	1993	50	0.28	0.38	0.34
	1994	49	0.59	0.20	0.20
Burned sagebrush (7b)	1993	50	0.10	0.52	0.38
	1994	50	0.34	0.60	0.06

[a] $n < 50$ indicates that the tag marking ≥1 burrow entrance was not found, so the fates of these entrances were unknown.

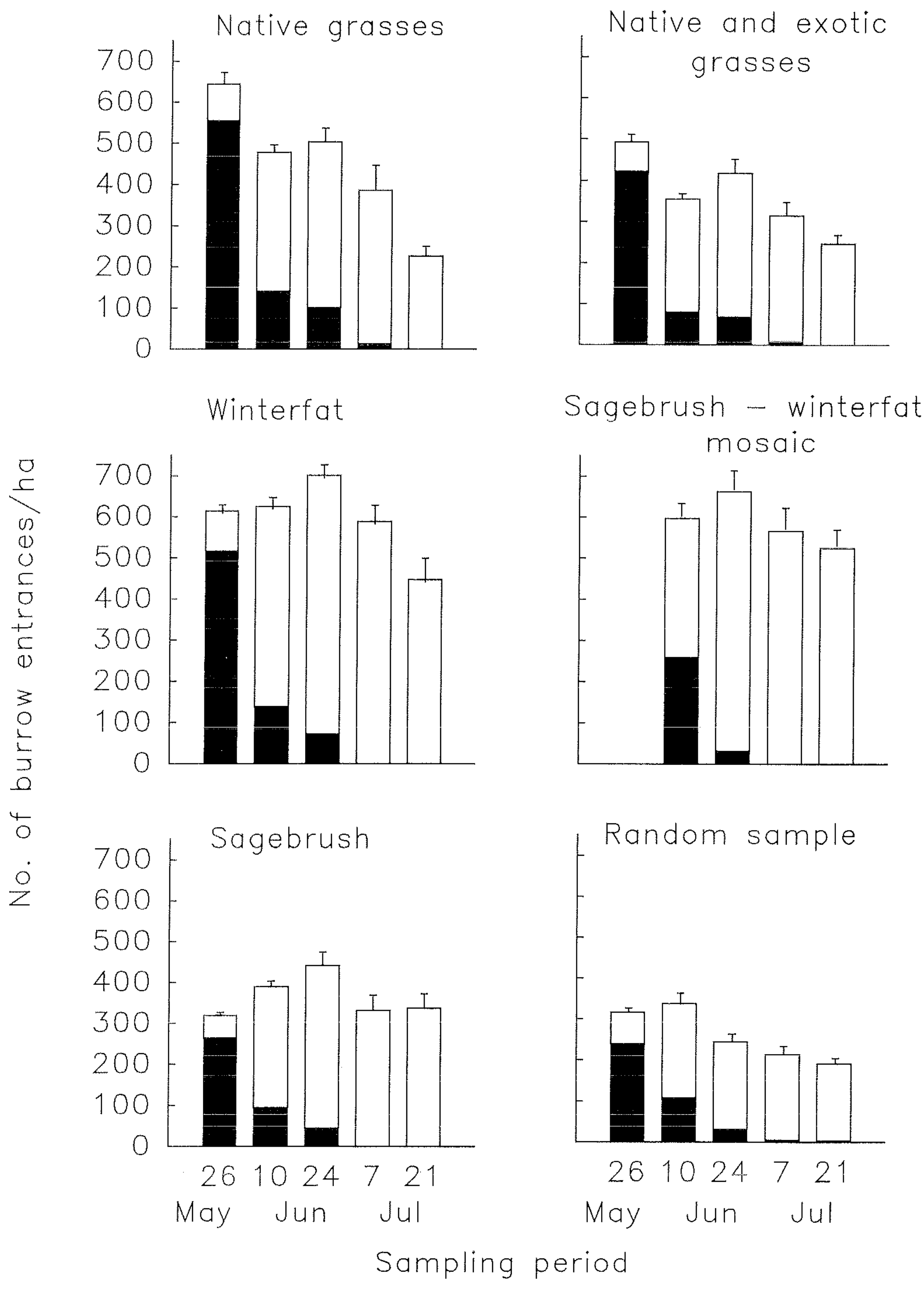

Fig. 2. Changes in total numbers (± SE) of burrow entrances during 2-week intervals between 18 May and 28 July 1992 on calibration transects in 5 habitats and on random sites throughout the Snake River Birds of Prey National Conservation Area. Total number is the sum of active (filled bars) and inactive (open bars) burrow entrances counted. Counts from random sites are means of all sites sampled within the 2-week periods.

DISCUSSION

We detected little relation between densities of burrow entrances and densities of ground squirrels, which is similar to results of Powell et al. (1994) for another sciurid species, the black-tailed prairie dog (*Cynomys ludovicianus*). These findings contrast with the predictability of ground squirrel densities indicated in Nydegger and Smith (1986). Our study was more extensive because we sampled more sites and our analysis included a greater range of squirrel densities. In addition, we used annual estimates of densities, whereas Nydegger and Smith (1986) used 5-year averages.

Our comparisons of burrow entrance and ground squirrel densities did not reveal a positive and consistent linear relation within habitat types. Although comparisons across habitats were significant, the slope of the relation for active entrances differed among years. Significant regressions were the result of combining data from shrub habitats with low ground squirrel densities and few burrow entrances with burned habitats supporting high ground squirrel densities and many burrow entrances. Placing the data in broad categories (high, medium, and low densities of burrow entrances) would not have significantly improved the weak relation we observed between burrow entrance and squirrel densities. A reasonable index of squirrel density should, at a minimum, detect major increases or decreases in squirrel populations between years. Burrow entrance counts did not accomplish this objective.

Several factors may underlie this weak relation between burrow entrance counts and ground squirrel densities. First, despite among-observer consistency in classification, we are not convinced that entrances to Townsend's ground squirrel burrows can be distinguished reliably from those used by other small mammals. Our sampling design for quantifying observer bias cannot be used to detect consistent biases, such as those resulting from incorrect criteria for classification or from use of burrows by multiple species. Incidental observation during the study indicated that ground squirrels may use burrow systems primarily attributable to kangaroo rats, and kangaroo rats and least chipmunks may use ground squirrel burrow systems. As part of a concurrent observational study, we observed ground squirrels using burrow entrances with morphology typical of kangaroo rat entrances (sandy areas, horizontal entrances, tail drags). We counted large numbers of apparent Townsend's ground squirrel burrow entrances in areas with few or no ground squirrels. Also, we blocked entrances of apparently active Townsend's ground squirrel burrows with sticks and debris on sagebrush sites and these barriers were sometimes opened with small holes about the size of a chipmunk. Appropriation of parts of burrow systems by other species may be particularly common when 1 species declines in density. Where this occurs, population estimates based on active burrow entrances will overestimate animal density after a general population decline.

Second, persistence of burrow entrances after a decline in ground squirrel density between years may result from use of more entrances by individual ground squirrels when population densities are low, use of ground squirrel burrows by other species when ground squirrel densities are low, or persistence of burrow entrances independent of use. Such persistence would lead to an underestimate of the magnitude of a population decline. Third, burrow entrances may persist differently among habitat types, independently of ground squirrel density. This difference is probably related to habitat characteristics such as shrub cover, which influences wind patterns above ground and soil stability below ground, and soils, as entrances in sandy soils would be more likely to cave in or be obscured by wind-blown sand. Weather may also affect persistence, as dryness and wind would decrease persistence.

Finally, calibration transects demonstrate that burrow entrance counts vary substantially over a short period of time when that period includes the immergence period. Conducting counts earlier in the season, however, would miss the peak of juvenile activity. To establish correction factors for single samples from concurrent calibration transects would be difficult. Inconsistency of calibration transects may partly reflect interactions among habitats, local-regional weather patterns, and timing of immergence in determining short-term burrow entrance dynamics. Because of these factors, counts of total burrow entrances are less variable temporally and among observers than are counts of active entrances.

MANAGEMENT IMPLICATIONS

We suggest that densities of burrow entrances are weak and potentially misleading indicators of Townsend's ground squirrel population densities in the SRBOPNCA. In our study, densities of burrow entrances did indicate the direction of a sharp between-year population decline, but a series of smaller, incremental declines might not be detected, given the loose linkage between burrow entrances and ground squirrel densities. Habitat biases in persistence render burrow entrance counts largely ineffective for describing among-habitat differences in ground squirrel density. They therefore do not provide an effective basis for predicting the result of management decisions that are linked to habitat change. Mark-recapture methods may provide more useful information on differences in ground squirrel densities among years and habitats for a given level of research effort, even when the objective is to obtain indices of change or difference rather than absolute density estimates.

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